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THE SCALE INSECT GENUS SMILACICOLA, WITH PARTICULAR REFERENCE TO ATAVISTIC POLYMORPHISM IN THE SECOND INSTAR (HOMOPTERA: COCCOIDEA: DIASPIDIDAE)

By SADAO TAKAGI

Abstract

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The genus *Smilacicola* is revised, and 3 species are referred to it: *S. crenatus*, n. sp., from Hongkong, *S. heimi* (=*Rugaspidiotus heimi*), n. comb., from Vietnam, and *S. apicalis* from Taiwan. The taxonomic position of the genus is discussed. Analysis of adult female characters shows that *S. crenatus* approximates the form ancestral to the other species. The 2nd instar males of all the species are parlatoriine in structural pattern. The 2nd instar female of *S. crenatus* is also parlatoriine, but differs in lacking gland tubercles. The parlatoriine larvae are supposed to represent an ancestral form of the adult females. The 2nd instar females of *S. heimi* and *S. apicalis* differ from them in lacking marginal appendages and gland tubercles and in the ducts showing a geminate pore structure at the inner end. They are subdivided into discrete forms. *S. crenatus* should be primitive as to the sexual dimorphism of the 2nd instar, too. The geminate pore type 2nd instar females of the other species are derived in this context. On the other hand, they are reminiscent of palm scales, which are more primitive than most other diaspidids, so that their appearance in the relatively derived species is interpreted as atavistic. The change of the 2nd instar females from the parlatoriine to the geminate pore type, extrapolated from a similar case in *Fiorinia*, is deemed to have occurred in a discontinuous manner. Genetic possibility for such phenotypic changes is suggested on the basis of a theory recently proposed for the genomic regulation systems of higher organisms.

Author's address. Entomological Institute, Faculty of Agriculture, Hokkaidô University, Sapporo, 060 Japan.

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Introduction

The genus *Smilacicola* has attracted my particular interest since it was erected, because, while referred to the Rugaspidiotini, it manifested an obvious pattern of the Parlatoriini in the 2nd instar male of the type-species. Three species of the genus I have examined, however, show that there is actually a complicated pattern of polymorphism in the 2nd instar. I have been, therefore, anxious to get further material of the genus for a more secure basis of my reasoning on this polymorphism. The three species come from Taiwan, Hongkong and Vietnam and are probably exclusively associated with *Smilax*, which is widely distributed in the tropics and subtropics. In my recent trips to Nepal and India, however, I collected no material of *Smilacicola* after all my effort. Further forms will most probably be found in southern China and highlands of eastern Indochina. Since these areas are not accessible to me at present, I would like to publish my study as a provisional report on the genus and the 2nd instar larval polymorphism.

Arguments advanced in this paper may appear to be too speculative. Morphoclinal analysis attempted is unsatisfactory owing to deficiency of material. But I think that the result of the analysis is plausibly interpreted on extrapolation from a similar case in *Fiorinia*, which was studied on the basis of more abundant material. I present here, I believe, what is probable in the limits of our recent understanding as to regulatory mechanisms in gene activity on one hand and constraints in developmental pathways on the other hand–'atavistic polymorphism'.

Smilacicola

Smilacicola Takagi, 1969, Insecta Matsumurana 32:55 [type-species: *Smilacicola apicalis*, occurring in Taiwan; it was suggested that 2 other species, *Rugaspidiotus heimi* from Vietnam and an unnamed species from Hongkong Is., also belong to the genus].

Composition. I have examined 3 species referable to the genus: *S. apicalis* from Taiwan, *S. crenatus*, n. sp., from Hongkong, and *S. heimi* (=*Rugaspidiotus heimi*) from Vietnam. The former two were collected on plants of *Smilax* (Liliaceae), occurring under the stipules. The last species was described as occurring on an undetermined vine, which is probably a *Smilax* species (see under *S. heimi*).

Adult female. Body elongate pyriform, roundly dilated in cephalothorax, gradually narrowing posteriorly in prepygidial abdominal segments, which are little lobed laterally; pygidium composed of 6th and succeeding abdominal segments, roundish or rather trapezoid, crenate or irregularly incised marginally, lacking any distinct appendages such as lobes, plates or gland spines, the apical region (belonging to 8th segment) produced in a low, broad prominence in 2 species (*S. apicalis* and *S. heimi*). Anal opening situated near base of pygidium, surrounded by a thick, strongly sclerotized ring. Derm strongly sclerotized posteriorly to anal and vulvar openings, striate or reticulate in the sclerotized region. Antennae situated halfway between anterior end of body and mouth-parts, separated from each other by more than width of mouth-parts, each composed of a low tubercle and 6 thick setae, of which four are usually longer and thicker than the other two. Anterior spiracles each with disc pores in a cluster; posterior spiracles with or without them; these disc pores are obviously 5-locular when seen in oil-immersion phase-contrast microscopy. Gland tubercles present on ventral surface anterolateral to anterior spiracle in 1 species (*S. crenatus*).

Ducts variable in size among species and between surfaces, short, 2-barred at inner end, and with a thick rim around orifice; numerous and strewn on both surfaces of pygidium, and also in prepygidial abdomen at least along body margin. Perivulvar disc pores absent.

Second instar larva. The 3 included species as a whole show a remarkable polymorphism in the 2nd instar larvae, which are divided into 2 main types called 'parlatoriine type' and 'geminate pore type' in the following lines.

The parlatoriine type, represented by the 2nd instar males of the 3 species and the 2nd instar female of *S. crenatus*, has well-developed lobes, all unilobed, and plates, each with an associated microduct; median lobes rounded apically, incised laterally, separated by 2 plates between; 2nd lobes similar to the median; 3rd lobes more or less similar to adjacent plates; plates occurring as anteriorly as base of abdomen and, in the males, replaced there by gland tubercles, which also occur on the thorax (gland tubercles absent in the 2nd instar female of *S. crenatus*). Macroducts short, 2-barred at inner end, with a thick rim around orifice, dorsal ones forming more or less of segmental rows. In the parlatoriine 2nd instar female of *S. crenatus* dorsal macroducts are much reduced in size except those occurring in posterior segments; there are no ventral macroducts. In the 2nd instar males, all of the parlatoriine type, the dorsal macroducts are not reduced in size both submedially on the abdomen and marginally and submarginally on the abdomen and thorax; ventral macroducts as large as dorsal ones, strewn on cephalothorax laterally to gland tubercles.

The geminate pore type, restricted to the 2nd instar females of *S. apicalis* and *S. heimi*, is much simpler in structure, lacking any distinct marginal appendages; the ducts, though variable in size, are of another type, being short and with a geminate pore structure at the inner end, and strewn.

In both types the pygidium appears to be composed of the 6th and succeeding segments as in the adult females, the 5th segment being well marked off in most forms of this instar. Antennae with 6 setae as in adult females; anterior spiracles with disc pores, posterior spiracles with or without them. Anal opening situated about middle or towards base of pygidium, surrounded by a thick sclerotized ring.

Second instar females oblong or, in a form of the geminate pore type (occurring in *S. heimi*), nearly circular in body shape at first, eventually growing pyriform with cephalothorax swollen. Exuviation takes place by the splitting of the derm along the suture between the dorsal and ventral surfaces of the pygidium, and the exuvial cast encloses the cephalothorax of the adult female even when this has fully grown.

First instar larva. Body elliptical. Head without enlarged dorsal ducts. Antennae 6-segmented, the terminal segment much shorter than the preceding segments united and not annulate. Anal opening situated just at posterior extremity of body, surrounded by a slender but strongly sclerotized ring. There is along the posterior margin of the abdomen a series of appendages, among which a pair of robust, sclerotized processes occurring just laterally to the caudal setae may be median lobes, being similar in shape to the median lobes of the parlatoriine 2nd instar larvae; a pair of broad, dentate processes or plates occurring between the supposed median lobes, and some processes laterally to the lobe. Single microducts occurring along body margin, 1 on each abdominal segment, the posteriormost situated just mesally to the median lobe; a few others in thoracic region. In

sclerotized exuvial casts the occurrence of plates can be traced as far as the prepygidial abdomen, where a much reduced plate is associated with the marginal microduct of each segment.

Smilacicola crenatus, new species

Material. Hongkong Is., on *Smilax* sp., 23 April, 1965. Mounted specimens includes 15 adult females, 2 2nd instar females, 4 2nd instar males, and some exuvial casts. Holotype (adult female) deposited in the collection of the Entomological Institute, Hokkaidô University, Sapporo.

Adult female (Figs. 7, 8, 10). Pygidium roundish, but a little pointed apically, crenate on whole margin, irregularly reticulate on dorsal surface, and striate on ventral surface except around vulvar opening; with a pair of setae apically. Anterior spiracle with 12–29 disc pores; posterior spiracle with none. A longitudinal cluster of 11–ca 37 gland tubercles present anterolaterally to anterior spiracle (in 1 specimen 4 gland tubercles are found just in front of the mouth-parts in addition to 36 tubercles occurring on one side and 27 on the other in the usual position). Dorsal macroducts of pygidium fairly large, with rim of orifice elliptical. Similar macroducts strewn in prepygidial abdominal segments along body margin, dorsally on 5th and preceding segments and ventrally on 4th and preceding segments. Much smaller ventral ducts strewn on pygidium except around vulvar opening, and also on prepygidial abdominal segments mostly in a broad submarginal region and, on 4th and preceding segments, mesally to macroducts. Seven submarginal dorsal bosses present on each side of body, the anteriormost on prosoma, the 2nd anteriormost probably situated between metathorax and 1st abdominal segment, the other five on succeeding intersegmental borders (or supposed borders), the posteriormost occurring between 5th and 6th abdominal segments; those occurring on prosoma, between 1st and 2nd abdominal segments and between the 3rd and 4th usually geminate, the paired elements of the prosomal boss separated from each other or appressed together (another boss may be present between the 6th and 7th segments, but is not discernible owing to the dermal reticulation).

Second instar female (Figs. 1, 9, 11). Belonging to the parlatoriine type, but lacking gland tubercles. Antennae situated near anterior ends of mouth-parts, separated from each other by width of mouth-parts. Anterior spiracles each with 5–23 disc pores (16 and 23 disc pores in 1 specimen, and 12 and 13 in the other; 5–20 in exuvial casts); posterior spiracles without disc pores. Dorsal macroducts variable in number and occurrence, but there is always 1 macroduct between the bases of the median lobes; in one extreme of variation macroducts occurring on 2nd (or 3rd) - 7th abdominal segments in margino-submarginal region and on 4th (or 5th) - 6th in submedian region (1 in each submedian series), over 30 in total, other ducts much slenderer, occurring as anteriorly as thoracic region in margino-submarginal region; in the other extreme only 1 macroduct is present on either side on the 7th abdominal segment on or near the margin in addition to the macroduct occurring between the median lobes, other ducts being all replaced by slender ones. Microducts abundant on ventral surface especially on cephalothorax along margin and also laterally to anterior and posterior spiracles. Eight bosses on each side of body near margin; the anteriormost occurring on prosoma and geminate, the 2nd anteriormost between metathorax and 1st abdominal segment, and the other six on the succeeding intersegmental borders (or supposed

borders), the posteriormost being supposed to be situated betweent the 6th and 7th segments.

Second instar male (Figs. 2, 9, 11). Antennae situated between anterior end of head and mouth-parts, separated from each other by a little more than width of mouth-parts. Anterior spiracles each with 7–13 disc pores; posterior spiracles without disc pores. Number of submedian dorsal macroducts on one side: 0–2 on 1st abdominal segment, 1–2 on the 2nd, 2–3 on the 3rd–5th each, and 0–2 on the 6th, total 9–12; 1 dorsal macroduct present or absent between bases of median lobes, 1 near margin on 7th abdominal segment, with or without another macroduct just anteriorly, other macroducts occurring dorsally in margino-submarginal region as anteriorly as mesothorax and ventrally along margin in thoracic region. Number of gland tubercles on one side: 5–8 lateral to anterior spiracle, 3–5 on mesothorax, 1–4 on metathorax, and 2–3 on 1st abdominal segment, total 13–20.

Smilacicola heimi, new combination

Rugaspidiotus heimi Balachowsky, 1947, Bulletin de la Société Entomologique de France 52:21 ["Récolté à Bah-Nah, 1400 m. env. de Tourane (Annam), ... sur une liane ampelidée indeterminée"].

Rugaspidiotinus heimi: Balachowsky, 1953, Les Cochenilles VII: 28 ["Le g. *Rugaspidiotinus* nov.,...., comprend actuellement 3 espèces: *circumdatus* Ferris, (génotype), *fuscitatis* Ferris, décrits de Basse Californie (Mexique) et *heimi* Balachw., d'Indochine"].

Material. Near "Tourane", now Da Nang, Vietnam, 1450 m, 24 February, 1939. Over 50 adult females, ca 30 2nd instar females, 10 2nd instar males, some 1st instar larvae and exuvial casts mounted from the type-material (all returned to the Muséum National d'Histoire Naturelle, Paris). These specimens were found mining in a thick mass of fungi (*Septobasidium xylostroma*, after Balachowsky) on 3 short pieces of host-plant's stem. The host-plant, "une liane ampelidée", is probably a *Smilax* species. This is strongly suggested by the stem pieces I examined and moreover *Smilax* occurs in Vietnam.

Adult female (Figs. 12, 13). Described in detail by Balachowsky. He writes: "Antennes à mamelon faiblement saillant surmonté d'une touffe de 7 à 8 soies; soies sensiblement égales entre elles....". In my examination of the newly mounted specimens the antennal setae are always 6 in number; they are practically the same in length, but often one or two among them are less developed than the others. Anterior spiracle with 28–86 disc pores (based on 22 spiracles); posterior spiracle with 13–40 (based on 58 spiracles). Numerous microducts strewn on prosoma in a longitudinal cluster extending laterally to antenna and anterior spiracle. "Zone médiane formée par le segment 8, large et légèrement saillante". This apical prominence of the pygidium is, however, variable in development: sometimes it is rather remarkable (Fig. 12) and similar to that in *S. apicalis*, but more often it is only slightly developed (Fig. 13).

Second instar female (Figs. 3, 4). Represented by 2 discrete forms both belonging to the geminate pore type. In one of them (Fig. 3) the body is oblong at first, with the pygidium sparsely and irregularly incised marginally and produced apically into a low, broad prominence; at full maturity this prominence is not visible and the pygidial margin is smoothly rounded. Mouth-parts situated as usual; antennae situated near to anterior lateral ends of mouth-parts. Anterior

spiracle with over 60–ca 90 disc pores; posterior spiracle with 29–55. Ducts somewhat variable in size, but all small, usually there are ducts which are somewhat larger than others and obviously show a geminate pore structure at the inner end; variable also in number, but usually limited to cephalothorax (in 1 specimen limited to cephalothorax and 1st abdominal segment), the larger ducts often quite few and sometimes not discernible on one or either side.

In the other form (Fig. 4) the body is nearly circular at first, with the mouth-parts situated towards centre of the body. Antennae situated on the level of mouth-parts, but much removed from mouth-parts, approaching body margin. Anterior spiracle with 15–ca 38 disc pores; posterior spiracle with 9–26 (in 1 specimen only 4 disc pores are associated with the posterior spiracle on one side, while 15 on the other side). Ducts variable in size, but all of them clearly show a geminate pore structure at inner end; numerous, strewn on ventral surface, except in a broad median region of head and on posterior abdomen, and also on dorsal surface along body margin.

These forms were found together on the short pieces of the stem of the host-plant, and there are no grounds for considering that the adult females, mounted from the same pieces, represent more than 1 species. I have no doubt that the 'oblong' and 'circular' forms of the 2nd instar females both belong to the same species.

Second instar male (Fig. 5). Body obovate. Antennae situated between anterior end of head and mouth-parts, separated from each other by a little more than width of mouth-parts. Anterior spiracle with 4–12 disc pores; posterior spiracle with 1–7. Number of submedian dorsal macroducts on one side: 1–2 (rarely 0) on 2nd abdominal segment, 2–5 on the 3rd, 2–4 on the 4th, 1–4 on the 5th, and 0–1 on the 6th, total 7–13. Other macroducts occurring dorsally along margin around abdomen and metathorax, and ventrally on thorax laterally to gland tubercles. Number of gland tubercles on one side: 15–18 in a nearly continuous cluster on prosoma, 3–7 on metathorax, 3–5 on 1st abdominal segment, total 22–29.

First instar larva (Fig. 6). General characters as described for the genus. (No definite specific characters are given here, because no detailed comparisons are possible with the other species, in which this stage is represented only by exuvial casts.)

Smilacicola apicalis

Smilacicola apicalis Takagi, 1969, Insecta Matsumurana 32: 55 [Taiwan, on *Smilax* sp.; adult female described, and adult female, 2nd instar male and female, and 1st instar larva (parts) illustrated.]

Material. Ken-ting, Taiwan, on *Smilax* sp., 2 April, 1965. In addition to the type-series some specimens were newly mounted from the type-material. The mounted specimens examined include 8 adult females, 15 2nd instar females, and 11 2nd instar males.

Adult female (Fig. 14). Apical prominence of pygidium always well developed. Anterior spiracle with 10–26 disc pores; posterior spiracle with 3–17. In some specimens microducts are obviously strewn behind the posterior spiracles and also in a zone around the posterior end of the mouth-parts and anterior spiracles, though they appear variable in number.

Second instar female. Similar to the oblong 2nd instar female of *S. heimi*, but with many ducts of the geminate pore type strewn over body except in middorsal region. Antennae situated in front of mouth-parts, separated from each other by a little more than width of mouth-parts. Anterior spiracle with 8–23 disc pores; posterior spiracle with 4–13. Pygidial margin rounded and crenulate.

Second instar male. Antennae situated halfway between anterior end of head and mouth-parts, separated from each other by width of mouth-parts. Anterior spiracle with 4–8 disc pores; posterior spiracle usually without disc pores (in 1 out of the 11 specimens examined a single disc pore is found at the right posterior spiracle). Number of submedian macroducts on one side: 1–2 on 2nd abdominal segment, 2–3 on each of the 3rd–5th, and 1 (rarely 0) on the 6th. Other macroducts occurring dorsally all around abdomen and thorax, and ventrally on thorax laterally to gland tubercles. Between the bases of the median lobes there are 2 marginal macroducts and, in front of them, 0–2 submarginal macroducts (when there occurs only 1 submarginal macroduct, it is always one-sided in position). Number of gland tubercles on one side: 5–10 lateral to anterior spiracle, 3–8 on mesothorax, 2–5 on metathorax, and 2–4 on 1st abdominal segment, total 13–26.

Taxonomic position of Smilacicola

The genus *Smilacicola* may be referred to the tribe Rugaspidiotini (or the subtribe Rugaspidiotina of the tribe Odonaspidini) in the current classification of the Diaspididae. The concept and composition of this tribe (or subtribe), however, appear to be problematical. So far as the adult females are concerned, *Smilacicola* is similar to *Rugaspidiotinus*, which appears to be distinct from *Rugaspidiotus* and comprises 3 North American species, *R. circumdatus*, *R. fuscitatis* and *R. nebulosus*. In the 1st instar larvae some noticeable differences are present between *Smilacicola* and *Rugaspidiotinus*: for example, in *Smilacicola* the antennae are 6-segmented, while in *Rugaspidiotinus* 5-segmented. In my examination of the adult female of *R. fuscitatis* I have noticed that the spiracular disc pores are clearly 3-locular, whereas in *Smilacicola* these pores are exclusively 5-locular. Borchsenius (1966) referred 7 Old World genera to the Rugaspidiotina, Odonaspidini. None of them appear to be particularly closely related to *Smilacicola*. Among them, *Natalaspis* (=*Poliaspoides*) may have some relationship to *Smilacicola*, but it also disagrees with the latter in having 5-segmented antennae in the 1st instar larva and 3-locular spiracular disc pores in the adult and 2nd instar females. Reliable information as to the occurrence of different types of spiracular disc pores (different in the number of loculi) in the family is still limited. But the differences mentioned are sufficient to throw doubt whether *Smilacicola* is really so closely related to *Rugaspidiotinus* and *Natalaspis* as expected from their similarity in the adult females.

Smilacicola has well-developed marginal processes, interpreted as lobes and plates, in the 1st instar larvae in spite of the absence of definite marginal appendages in the adult females. It also shows good lobes and glanduliferous plates in the 2nd instar males of all the species and the 2nd instar female of *S. crenatus*, and the pattern of characters these larvae present conforms to that of the Parlatoriini (excluding the leucaspidines, in which the pygidial plates are not glanduliferous) except for the fewer segments composing the pygidium and the multisetose antennae.

It seems, therefore, apparent that *Smilacicola* is closely related to the Parlatoriini in some way. The parlatoriine pattern, manifested by both the 2nd instar larvae and the adult females in the Parlatoriini, is also traceable in the adult females of *Smilacicola*, though much obscured probably owing to secondary modification. In this regard this genus must be derived compared with that tribe. Difficulties in accepting this view are that in *Smilacicola* the pygidium is composed of fewer segments and the antennae are multisetose in the 2nd instar larvae as well as in the adult females, and, thus, the genus is apparently more primitive than the Parlatoriini. (In the corresponding stages of the Parlatoriini the 5th abdominal segment is also part of the pygidium, as based on the fusion in the margino-submarginal region, and the antennae are unisetose.) But this does not preclude supposed relationship of *Smilacicola* to the Parlatoriini. The simplest explanation here may be that *Smilacicola* is immediately related not to the Parlatoriini themselves but to forms ancestral to them. The 2nd instar females of *S. heimi* and *S. apicalis* manifest other patterns, belonging to the geminate pore type. (But they agree with the parlatoriine-type larvae in the segments composing the pygidium and the antennae having as many as 6 setae). This also needs an explanation, but does not necessarily afford evidence against the supposed affinity with the Parlatoriini, either.

Odonaspis is another genus in which the parlatoriine pattern is clearly manifested in the 2nd instar (at least in the males of 2 species) and suppressed in the adult females (except for the occasional occurrence of gland tubercles) (see under Second instar larval polymorphism in other diaspidids). *Smilacicola* is undoubtedly related to *Odonaspis* and, therefore, to the Odonaspidini, but the relationship is not traceable further at present. Extensive studies of the 2nd as well as 1st instar larvae are necessary in order to find the true taxonomic positions of the Odonaspidini and the supposed Rugaspidiotini.

Relationship among the species of Smilacicola

The 3 species referred to *Smilacicola* closely resemble one another in the external characters of the adult females, 2nd instar males and 1st instar larvae, and there seems to be no doubt that they are closely related phylogenetically. Characters of the 2nd instar females, however, are not uniform, showing a remarkable difference between *S. crenatus* and the other 2 species. I will try to give an explanation for this phenomenon, adopting the view that the 3 species are really closely related. Further, this view is supported by their distribution (Taiwan; Hongkong; Vietnam) and known or supposed host-plants (*Smilax* spp.).

Since the adult females are very similar in general structure, characters distinguishing them are limited. The pygidial margin is remarkably crenate in *S. crenatus*, finely crenulate in *S. heimi*, and smooth, with sparse irregular incisions, in *S. apicalis*. Although these characters suggest diverging rather than successively changing states, they may be arranged in the mentioned order in terms of the decreasing ruggedness of the pygidial margin (morphocline I). In *S. crenatus* some apical crenations are eminently lobed, but none of the crenations are definitely identifiable as the usual lobes or other marginal appendages. It is possible, however, that the crenations are really reduced and modified lobes and plates, because these appendages are well developed in the preceding instars. On this supposition

the state in *S. crenatus* may be taken for a primitive character in comparison with the less rugged or smooth margin in the other species.

The apical region of the pygidium, presumably belonging to the 8th abdominal segment, is produced to form a broad prominence in *S. apicalis*. A similar prominence is seen in *S. heimi*, in which, however, it is variable in development and usually much less remarkable. In *S. crenatus* the projection of the same region is nothing more than a mere suggestion. The rectangular prominence in *S. apicalis* is quite unique, so that a morphocline may be constructed for the tendency towards apical projection (morphocline II). There is a similar tendency in the North American *Rugaspidiotinus*. This suggests some relationship between these genera; otherwise, parallelism should be considered. It seems that in association with the projection some setae in the region are displaced in both genera.

In *S. crenatus* gland tubercles are present on the prosoma, and they are possibly a remnant of the parlatoriine features. In the other species microducts are strewn where gland tubercles are expected, suggesting reduction of gland tubercles to microducts (morphocline III).

The ducts are variable among the species. The dorsal macroducts of the pygidium are comparatively very large in *S. crenatus*, being similar to those in the parlatoriine-patterned 2nd instar. This character should be primitive in comparison with the much smaller dorsal ducts in the other species (morphocline IV). The ventral ducts of the pygidium are minute and obviously smaller than the dorsal ones in *S. crenatus* and *S. apicalis*; in *S. heimi* the ducts are of the same size on both surfaces and are not so small as the ventral ducts of the other species except for the minute ducts occurring along the margin on both surfaces (morphocline V). There seems to be no *a priori* basis for determining polarity for all these states. The combined morphoclines IV and V suggest divergence among the 3 species rather than successive changes in them.

The prepygidial ducts of the abdomen are abundant, being strewn all over the segments, in *S. heimi*, while largely restricted to the marginal region in the other species (morphocline VI). The anterior spiracular disc pores are also more numerous in *S. heimi* than in the other species (morphocline VII). The posterior spiracular disc pores are more numerous in *S. heimi* than in *S. apicalis* and lacking in *S. crenatus* (morphocline VIII). The dorsal surface of the pygidium is elaborately reticulate in *S. crenatus*, rudimentarily so and only around the anal opening in *S. apicalis*, and finely striate in *S. heimi* (morphocline IX). Polarity is not determined for these morphoclines.

The 2nd instar males are all parlatoriine-patterned. They are very similar to one another except for the presence (in *S. heimi*) or absence (in *S. crenatus*, and also in *S. apicalis* with an observed exception) of disc pores at the posterior spiracles (morphocline X), slight differences in the number and occurrence of dorsal macroducts, and other subtle ones. There are available, therefore, few characters to construct morphoclines.

On the other hand, the 2nd instar females are so different between *S. crenatus* and the other species that no sequential changes are observed through them except in the numbers of the anterior and posterior spiracular disc pores (morphoclines XI and XII).

All the morphoclines discussed are summarized in Table 1. *S. crenatus* is found at the primitive extreme in the morphoclines for which polarity is

Table 1. Morphoclines constructed for major distinguishing characters among the 3 species of *Smilacicola* and sequence of species in each morphocline.

Morphocline	Sequence of species
I	*crenatus* → *heimi* → *apicalis*
II	*crenatus* → *heimi* → *apicalis*
III	*crenatus* → [*heimi* / *apicalis*]
IV	*crenatus* → [*heimi* / *apicalis*]
V	[*crenatus* / *apicalis*] — *heimi*
VI	[*crenatus* / *apicalis*] — *heimi*
VII	[*crenatus* / *apicalis*] — *heimi*
VIII	*crenatus* — *apicalis* — *heimi*
IX	*crenatus* — *apicalis* — *heimi*
X	*crenatus* ≑ *apicalis* — *heimi*
XI	*crenatus* ≑ *apicalis* — *heimi*
XII	*crenatus* — *apicalis* — *heimi*

Morphocline I–XII, see text; →, polarity; —, polarity undetermined.

determined and may approximate the form ancestral to the other species at least concerning the characters used to construct those morphoclines. However, the pattern presented in the table suggests, as a whole, divergence rather than ancestral-descendant relationship, especially between *S. heimi* and *S. apicalis.*

In the pygidial characters of the adult females *S. crenatus* is rather isolated and deemed to be primitive. It also differs from the other species in that both male and female of the 2nd instar are parlatoriine-patterned. In some other characters *S. heimi* is relatively isolated and possibly more derived in those characters.

Second instar larval polymorphism and its evolutionary implications

Second instar larval polymorphism in Smilacicola

The 2nd instar larval polymorphism in the 3 species of *Smilacicola* is summarized in Table 2. If the reasoning advanced in the foregoing section is right, *S. crenatus* should be primitive in the state of sexual difference in the 2nd instar, too, in comparison with the other species. I therefore postulate that in this genus the 2nd instar is originally parlatoriine in either sex. In this respect it may be curious that gland tubercles are absent in the 2nd instar female of *S. crenatus,* for they occur in the adult female of the same species in spite of its much modified state (in contrast with the supposed ancestral parlatoriine form). Gland tubercles are an important parlatoriine attribute, and their absence may show that the 2nd instar female of *S. crenatus* has already departed, to some degree, from the basic parlatoriine pattern.

Table 2. A summary of the 2nd instar larval polymorphism in *Smilacicola*.

	crenatus	*apicalis*	*heimi*
Second instar male	P1	P1	P1
Second instar female	P2	GO1	GO2 GC

P: parlatoriine type, with lobes and plates.
- P1: gland tubercles present; none of dorsal macroducts reduced in size; ventral macroducts present.
- P2: gland tubercles absent; dorsal macroducts much reduced in size except on posterior parts of body; ventral macroducts absent.

G: geminate pore type, without marginal appendages.
- GO: body oblong; antennae situated near mouthparts.
  - GO1: ducts strewn except in middorsal region.
  - GO2: ducts more or less restricted to anterior end of body and sometimes much reduced in number.
- GC: body nearly circular; mouth-parts situated towards centre of body; antennae much dislocated laterally.

The geminate pore type 2nd instar females of *S. apicalis* and *S. heimi* should, accordingly, be derived. They are further divided into 3 forms, which are, however, commonly characterized by having geminate pore type ducts and by lacking any distinct marginal appendages. In the Diaspididae such ducts are limited to a small number of species (except for the enlarged dorsal ducts occurring on the head of the 1st instar larvae) and largely to palm scales, which are classified into a subfamily under the family Diaspididae or even into their own family (Phoenicococcidae in Borchsenius' catalogue, 1966). This type of ducts has generally been supposed to have originated from geminate pores, which are largely specific to the Asterolecaniidae and scattered in other families. The geminate pore type ducts are, therefore, primitive in comparison with the 1- or 2-barred ducts, which are found in a much larger part of the Diaspididae and do not occur in other families of Coccoidea. It would be but a short step to conclude that the palm scales (restricted to those forms with geminate type ducts and without any trace of marginal appendages) are relics of the diaspidid (or diaspidoid) stock. Stickney (1934) discussed in detail a supposed close relationship between the palm scales and the asterolecaniid genera *Mycetococcus* and *Capulinia*. (Later, *Capulinia* was assigned to other families by authors.) So far as based on external morphologies the relationship of the Diaspididae to the Asterolecaniidae has not yet been rejected (Danzig 1980). (Tubular ducts with a geminate pore structure at the inner end are found in the Beesoniidae, too, which are, however, an isolated group of unknown affinity.)

I am rather puzzled how to discuss the geminate pore type 2nd instar females of *Smilacicola*, because, unlike the parlatoriine-patterned larvae, there are no other

scale insects known to me closely agreeing with them in the pattern of characters. It may be reasonable to connect them with the palm scales. A difficulty in recognizing this connection is structural simplicity in both groups, which may cause a superficial similarity between them. Even so, there is, at least, no positive reason to reject the view that 2nd instar females of *S. apicalis* and *S. heimi* represent insects as primitive as the palm scales concerning the general structure of body.

The presence of the discrete forms in the geminate pore type is another problem. Above all, the circular form is peculiar in that the antennae are displaced from the usual position. I have no clear idea about this phenomenon except that the polymorphism may have an evolutionary explanation.

I have no idea if the different types of the 2nd instar females have their own adaptive significance, either. *S. crenatus* and *S. apicalis* occur under the stipules of the host plants, while *S. heimi* was found associated with the fungus *Septobasidium*. This difference is apparently not associated with the occurrence of the parlatoriine or geminate pore type. All these species agree in their cryptic mode of life.

Second instar larval polymorphism in other diaspidids

In general, coccoid larvae are very similar between the sexes and the adult females are larva-like in appearance. This fact, coupled with decreased growth stages in the females, has long been considered as evidence for the neotenic nature of the adult females.

In part of the Diaspididae remarkable sexual dimorphism has been found in the 2nd instar larvae (Boratyński 1953 and others). Our knowledge is still meagre as to its extent and patterns, but it seems to be restricted to the Diaspidini (excluding the lepidosaphedines), Rugaspidiotini and Odonaspidini. In still fewer cases the 2nd instar larvae of one sex greatly differ in structural characters between species belonging to the same genera, thus one part of such discontinuous forms also greatly differs from the 2nd instar larvae of the opposite sex.

In *Smilacicola* none of the polymorphic 2nd instar larvae are closely similar to the adult females. Yet the geminate pore type 2nd instar females agree with the adult females in lacking marginal appendages; the oblong form of *S. heimi* further approaches the adult female by having an apical prominence on the pygidium. In the foregoing lines it is suggested that the discontinuous larval forms represent successive ancestral forms of the adult females. This possibility will be discussed in connection with another case of polymorphism. The agreement between the geminate pore type 2nd instar females and the adult females already mentioned may also suggest that atavism has been involved in the evolution of the adult female.

Besides *Smilacicola*, 3 genera are known to be remarkably polymorphic in the 2nd instar.

(1) *Rhododendron*-associated species of *Fiorinia*, studied by me (Takagi 1975, 1979, 1980) (Table 3). This genus is pupillarial, the adult females being enclosed within the enlarged exuvial casts of the 2nd instar. The 2nd instar females are very similar to the adult females of the respective species in the characters of the pygidial margin. The 2nd instar males, known at least for 16 species, are largely divided into 2 strikingly different types: glandular and non-glandular types as named. There are variations in each type. Non-glandular 2nd instar males,

Table 3. Polymorphism in the 2nd instar males of *Fiorinia* in connection with a putative phylogenetic relationship among the *Rhododendron*-associated species (Takagi 1979).

Glandular type	Non-glandular type	
	Median lobes widely separated	Median lobes set close
hymenanthis —— (?) ——→	*sikokiana*	
↓		
odaiensis ——→	*nachiensis* Oki form ——→	*nachiensis* Kii form
? ——→	*horii*	
? ——	(?) ——→	*himalaica*
other spp.		

represented by 4 species (all associated with *Rhododendron* as given below), are somewhat diverse, but may be subdivided into forms with the median lobes widely separated from each other and those with the median lobes set close and definitely zygotic. The former are intermediate between the latter and the glandular type, because this also has widely separated median lobes (but otherwise bears no particular resemblance to those forms). The glandular males are quite different from, but the non-glandular ones, especially those with zygotic median lobes, are comparatively similar to, the 2nd instar females.

In Japan 5 species of *Fiorinia* are associated with *Rhododendron* (subgen. *Hymenanthes*), occurring on the undersurface, in the indumentum, of the leaves. So far as known, they are allopatric. Three of them are supposed to form a close approximation to an ancestral-descendant lineage: *hymenanthis*→*odaiensis*→*nachiensis*, Oki form→*nachiensis*, Kii form, because their adult and 2nd instar female characters vary within species and from species to species in such a manner as to produce a practically continuous series of intergrading forms. (The pattern of evolution suggested here, however, does not fit the model of phyletic splitting, but accords more harmoniously with the concept of punctuated equilibria, because succeedingly ancestral forms are presumed to have persisted without substantial morphological changes.) Among them, *F. hymenanthis* and *F. odaiensis* show no difference between them in the characters of the 2nd instar males, which belong to the glandular type. In the Oki form of *F. nachiensis* this stage is non-glandular and with separated median lobes, and in the Kii form of the same species non-glandular and with zygotic median lobes. All these forms of the 2nd instar males should also be in ancestral-descendant relationship in the mentioned order. Compared with the continuously varying female characters the change of the 2nd instar males from the glandular to the non-glandular type is impressively abrupt and discontinuous.

Another *Rhododendron*-associated species, *F. sikokiana*, may have derived from *F. hymenanthis* so far as based on the female characters, but there have been found no intervenients to connect them. The 2nd instar male of *F. sikokiana* is non-glandular and with separated median lobes. It is unique in that the median lobes are often subdivided into 2 lobules. The last species, *F. horii*, is isolated, without any known close relatives. It also has a non-glandular 2nd instar male with separated median lobes.

There are 2 or 3 other species of *Fiorinia* known to occur on *Rhododendron* in Taiwan and the Himalayan region. The Himalayan *F. himalaica* was studied in connection with the investigation of the Japanese species. Analysis of female characters shows that it is not related to any of the Japanese *Rhododendron*-associated species. In spite of this, it is identical with the Kii form of *F. nachiensis* in every external feature of the 2nd instar male. *F. himalaica* and the Kii form of *F. nachiensis* are both in the most derived state among the *Rhododendron*-associated species so far as the adult female characters are concerned.

The gradual changes observed for the female characters have very probably resulted from adaptive selection. It is presumed that the development of the median lobes into semicircular, elaborately serrate processes in the 2nd instar females has been adaptive in connection with the mining habit of the females. The numerical decrease of external secretory organs in the adult females must have been adaptive in connection with the pupillarial mode of life. The persisting ancestral forms and the allopatry of the species suggest that some local conditions, probably climatic, are also involved as factors in the causation of the changes.

The discontinuous changes of the 2nd instar males should be explained in connection with the continuous ones in the females. I (Takagi 1980) adopted the prepattern-precursor model to apply to the phenomena under discussion. The conclusion I arrived at was generalized in the statement that "a change induced by direct adaptive selection, while it is necessarily gradual, may give rise as its inevitable result to a discontinuous change, which primarily has no adaptive significance by itself." The close similarity between *F. himalaica* and the Kii form of *F. nachiensis* in the 2nd instar males was explained by "accepting the development of similar prepatterns in the epigenesis of the second instar males among members of the same genus, as well as a common effect of the much derived condition of the adult females on the phenotypic characters of the second instar males (because males and females share the same genetic base)." As to the taxonomic problems it was concluded that "we need not regard the series composed of *F. hymenanthis*, *F. odaiensis* and *F. nachiensis* as a mere coincidence of female characters, nor need we divide the genus *Fiorinia* as understood in the current concept into two unrelated genera." The phylogenetic meaning of the discontinuous forms of the 2nd instar males, however, was not brought out clearly.

(2) North American species of *Quernaspis*, studied by Howell (in Takagi & Howell 1977). Three species, all associated with *Quercus*, form a sequential series, *quercus — insularis — quercicola*, in some features of the adult females, while in the 2nd instar males they show a remarkable gap between *Q. insularis* and *Q. quercicola*. Morphoclines have not fully been analysed for them. (The Asian species once referred to *Quernaspis* were later removed to another genus, and there are now known to be no species of *Quernaspis* in the area.)

(3) A case in *Odonaspis*. The 2nd instar males of *O. penicillata* and *O. secreta* are definitely parlatoriine in appearance as illustrated by me (Takagi 1969) for the former species. Howell & Tippins (1978) described *O. minima*, which quite differs from them in completely lacking lobes and plates in the 2nd instar male. All these species may not be closely related to one another, yet the difference in the 2nd instar males is much greater than may be expected from the adult females. In having parlatoriine-patterned 2nd instar larvae the case here is very similar to that of *Smilacicola*, in which, however, the pattern change occurs not in the males but in the females.

In either of *Quernaspis* and *Odonaspis* the 2nd instar females resemble, and one of the discontinuous forms of the 2nd instar males more or less approaches, the adult females in at least the characters of the pygidial margin, agreeing with the condition found in *Fiorinia*. In the following lines I discuss, therefore, only the condition of *Fiorinia*, which was studied on the basis of more abundant material than in the other two.

Evolutionary implications

The genera *Fiorinia* and *Quernaspis* are classified in the Diaspidini, and *Odonaspis* in the Odonaspidini. *Smilacicola*, as stated, is referable to the Rugaspidiotini. A remarkable feature commonly observed in all these genera is a startling gap in the structural patterns of the 2nd instar males (in *Fiorinia*, *Quernaspis* and *Odonaspis*) or females (in *Smilacicola*) in contrast with the similar and, in 2 cases, continuously changing morphology of the adult females (or, in *Fiorinia*, of the adult and 2nd instar females). As far as the species in each genus are really so closely related to one another as indicated by the adult female morphologies and, therefore, really belong to the same genus at least, there must be a common base underlying the unusual phenomena observed in the 4 genera. On this premise the case in *Fiorinia* may be adopted as a paradigm for all the others.

I therefore propose that the different structural patterns observed in the 2nd instar females of *Smilacicola* could have arisen within the limits of the same genus and have changed discontinuously in the course of evolution. This change may have actually been carried out by some intermediates, which evolved rapidly. But it is also possible that individuals of the geminate pore type suddenly appeared in the transitional population, increased in frequency, and ultimately replaced those of the parlatoriine type. This possibility even appears plausible, when the concurrence of the 2 discrete forms in the 2nd instar female of *S. heimi* is taken into consideration. In the material examined, which probably originated from a single breeding colony, these forms appeared approximately with the same frequency (19 specimens of the oblong form and 12 of the circular one). They were also found in exuvial casts as may be expected, but the circular form was represented only by 1 out of 70 casts. There is evidently little probability that this difference between the the 2nd instar females and the exuvial casts is due to a chance. The difference should, therefore, imply either differential survival of these forms or change (or fluctuation) of their frequencies in generations. It is not possible to ascertain from the available data whether the population under consideration was in a transitional phase or in a stasis. The possibility is also not excluded that the change into the geminate pore type took place more than once, because the 3 species do not appear to represent successive stages in a lineage.

In the foregoing sections it is maintained that the parlatoriine-patterned 2nd instar larvae represent an ancestral form of the adult female, and also that the geminate pore type 2nd instar females imply a more primitive state. If these interpretations are right, the different patterns are successive manifestations of ancestral forms. The circular form of the geminate pore type, occurring in *S. heimi*, may be a reappearance of a presently unknown archaic form. At least it seems very probable that in the past the ancestor of *Smilacicola* was parlatoriine in the adult female and the male and female of the 2nd instar, fulfilling one condition required for the neotenic theory of female coccoid evolution. There is evidence for this view

in the adult female itself — the occurrence of gland tubercles in *S. crenatus*. The 1st instar larvae, which have well developed appendages (as in the Parlatoriini) in all the 3 species, also support the view.

The interpretations adopted for the 2nd instar larval forms of *Smilacicola*, on extrapolation from the case in *Fiorinia*, would suggest in turn that the appearance of the non-glandular 2nd instar males in *Fiorinia* is the recall of a pattern once suppressed in the course of evolution. Compared with the glandular males they approach the adult and 2nd instar females, and agree with the latter in having enlarged, semicircular, elaborately serrate median lobes. These lobes, quite unusual for the members of the genus, are presumed to have developed in different lineages in connection with the mining habit of the females in the indumentum of *Rhododendron* leaves. It is difficult to imagine that such lobes have any function in the 2nd instar males, which occur on the surface of the indumentum or, at least, do not mine so deeply as the females do.

An explanation for the occurrence of the enlarged median lobes in the 2nd instar males may be sought in the return of those males to the ancestral state in which the 2nd instar male is similar to the adult and 2nd instar females in structure. Thus, the supposed atavistic manifestation of phenotype in the 2nd instar males could have involved an evolutionary novelty (the enlarged median lobes) originally developed in the females. The situation is further complicated in the 2nd instar males of *Fiorinia sikokiana*, in which the enlarged median lobes are often divided into 2 lobules. This state is quite unusual for the Diaspididae. I (Takagi 1979) advanced the suggestion that all the lobes, including the median pair, tend to be bilobate in *Fiorinia* and other Diaspidini. I do not understand why this tendency has exceptionally been materialized for the median lobes of the 2nd instar males of *F. sikokiana*. Another conclusion deduced here is that the occurrence of the glandular 2nd instar males and, hence, the remarkable sexual dimorphism in the 2nd instar are only secondary.

Concerning the sexual dimorphism of the 2nd instar, therefore, it follows that *Smilacicola* started with the primary state, in which the male is very similar to the female, and the atavistic change gave rise to a remarkable sexual dimorphism. (*Odonaspis penicillata* and *O. secreta* may be in this secondary state of sexual dimorphism, and, if so, the state of the 2nd instar male of *O. minima* may have appeared in further change.) It also follows that in *Fiorinia* the evolutionary change started with a secondary state, in which sexual dimorphism is remarkable, and then brought in an approach to the ancestral state of dimorphism. Indeed, the glandular 2nd instar males occurring in *Fiorinia* and *Pseudaulacaspis* are quite strange in structure and find no counterparts outside the Diaspidini. They may have been produced as an oddity during the evolutionary course within the Diaspidini. (The 2nd instar males of *Quernaspis quercus* and *Q. insularis* and also of *Chionaspis*, *Aulacaspis*, etc., all belonging to the Diaspidini, show another pattern, which approaches to the glandular type by the marginal appendages ill developed and much deformed.)

Concluding remarks

I do not think that I have ascribed too much to atavism in the foregoing discussions. Atavism itself is an established concept and seems to be associated with extensive biological phenomena. Hampé (1959) operated on the hind leg

rudiments of chick embryos in a manner to prevent "compétition" between the developing tibia and fibula. The resulting pattern, quite deviating from the normal skeleton, was reminiscent of the *Archaeopteryx* or even reptilian condition. García-Bellido (1977) made a comparative analysis of the known types of homoeotic mutants in insects and discovered the existence of invariants in the homoeotic transformation. In most cases the affected organs are considered as phylogenetically more recent than the mimicked one, and "in this sense homoeotic mutations can be considered as atavic." Van Valen (1978) cited from Smith's thesis a supposed case of "a wholesale reversal of evolution, ecologically welcome if not quite predictable", in the fishes of the Snake River, Idaho. In plants Robson (1972) discussed "a case in *Hypericum* of what seems to be a genuine reappearance of an organ that was doubtless present in ancestral forms but not in primitive species of *Hypericum* itself". There is among developmental biologists a general agreement that we can "expect the reappearance of ancestral features and of the same novelties since we are dealing with regulation of resilient developmental programs" (Alberch, 1980).

The discontinuous manifestation of an ancestral state, interpreted as such in this paper, requires some regulatory system in the gene expression during development explainable in terms of sets of genes rather than individual gene activities and capable of maintaining ancestral phenotypic potential. Britten & Davidson (1969) advanced a model of overlapping batteries of genes "such that multiple change in gene activity can result from a single initiatory event" by the agency of interspersed repetitive nucleotide sequences. In this model "the regulation is accomplished by specific activation of *otherwise repressed sites,* rather than by repression of otherwise active sites" (italics mine). Davidson & Britten (1971) showed how the overlapping batteries of genes can act in cell differentiation. This model is not workable for the particular problem confronting us, but it may show what is generally expected for the regulatory system of higher organisms.

The Britten & Davidson model, therefore, may be applied to the cases in *Fiorinia* and *Smilacicola* only in a very generalized manner. There may be supposed batteries of genes which are variable in activity either in timing or according to species, generations or individuals and, when switched over at a particular time of development, bring about atavistic manifestation in the 2nd instar male or female. The patterns in replacement observed in the 2nd instar of *Smilacicola* and the phylogenetic interpretations adopted for them imply that there would be in the genome some order to induce successively more primitive phenotypic patterns. Activity responsible for manifesting a pattern should precede that inducing another more primitive one. Thus, the consideration here postulates some 'phylogenetic order' in the regulatory system. The convenient concept "prepattern" may now be considered in terms of the capacity of overlapping batteries of genes for promoting developmental processes.

Evolutionary changes may in principle be gradual, because any change should fulfill an internally consistent programme of development. Atavistic phenotypes, however, can literally be abrupt when they appear, because developmental pathways resulting in their manifestation must have been tested in the phylogenetic history of the organisms concerned for interaction and coordination at the genetic and epigenetic levels. (This consideration does not necessarily exclude the possibility that changes in regulatory network can occasionally give rise to programmes leading to the development of discontinuous but viable new structures.

Rather, as pointed out by Hunkapiller et al. (1982), cryptic maintenance of phenotypic potential suggests for the other side of the coin the possibility of large-scale phenotypic experiments.)

It was argued that changing phenotypic characters of the 2nd instar should involve neutrality or redundancy from the viewpoint of adaptation (Takagi 1980). This is possible in the Diaspididae, because the 2nd instar in the family is an exclusively trophic stage and its biological environment is, therefore, relatively relaxed. It is not wholly clear, however, why the stages affected are the males in *Fiorinia* and the females in *Smilacicola*. In *Fiorinia* it was presumed that adaptive selection in the females and especially in the 2nd instar females induced the discontinuous changes in the 2nd instar males. I have no idea how adaptation induced the atavistic changes in the 2nd instar females of *Smilacicola*.

After all, the view is not rejected that the manifestation of the atavistic pattern in the 2nd instar is in itself an effect or incidental consequence of adaptive selection. It is beyond the scope of this paper to proceed with an extended discussion about the evolutionary role of atavism. But I would like to point out the possibility that atavism may have been involved in the evolution of higher taxa. In the foregoing section the possibility is suggested that adult females of *Smilacicola* are atavistic in lacking marginal appendages. The African genus *Nimbaspis* is referable to the Rugaspidiotini. The adult females of this genus are also without marginal appendages and appear to be more archaic than those of *Smilacicola* owing to their ducts, which show a geminate pore structure at the inner end (Balachowsky 1958; Balachowsky & Ferrero 1967). If *Nimbaspis* is really closely related to *Smilacicola* and/or other rugaspidiotines, there is a possibility that an atavistic evolution was responsible for the appearance of the geminate pore type ducts in the adult female stage. The larvae of this genus, therefore, deserve to be studied in connection with the supposed atavistic origin of the genus.

All the phenomena presented above, however unusual, must be rooted in the general nature of the regulatory mechanisms of higher organisms. In this regard the generalization may be drawn that *derived organisms do not always appear more derived than their ancestral ones in every respect*. This generalization is based, on the other hand, on the expectation that even an atavistic organism may retain in its ontogeny some trace of its phylogenetic history despite the reappearance of ancestral characters. But, is there really any secure basis for this expectation ?

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PLATES

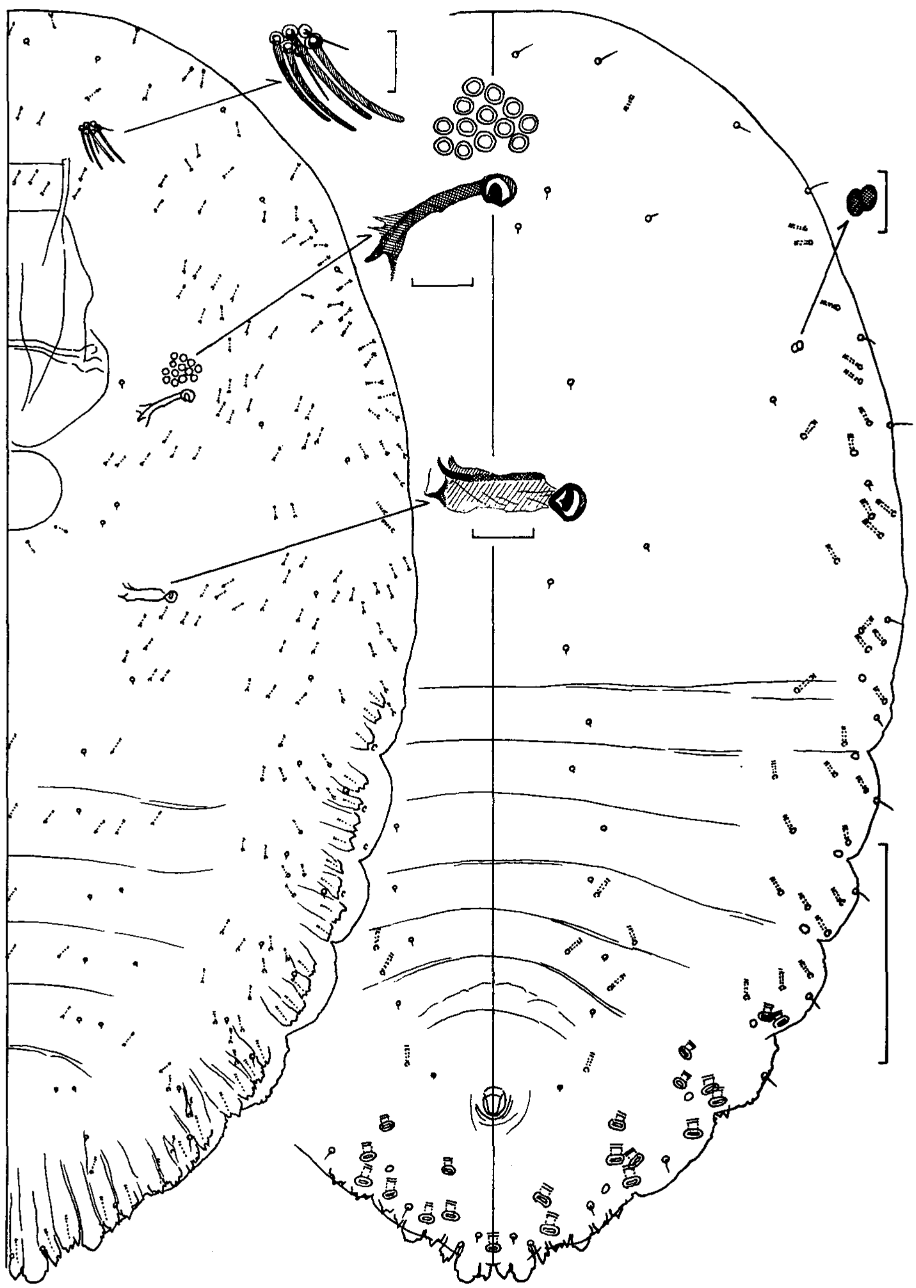

Fig. 1. *Smilacicola crenatus*, n. sp., 2nd instar female. Scale for body, 0.1 mm; scales for parts, 0.01 mm.

Fig. 2. *Smilacicola crenatus*. n. sp., 2nd instar male. Scale for body, 0.1mm; for antenna, 0.01 mm.

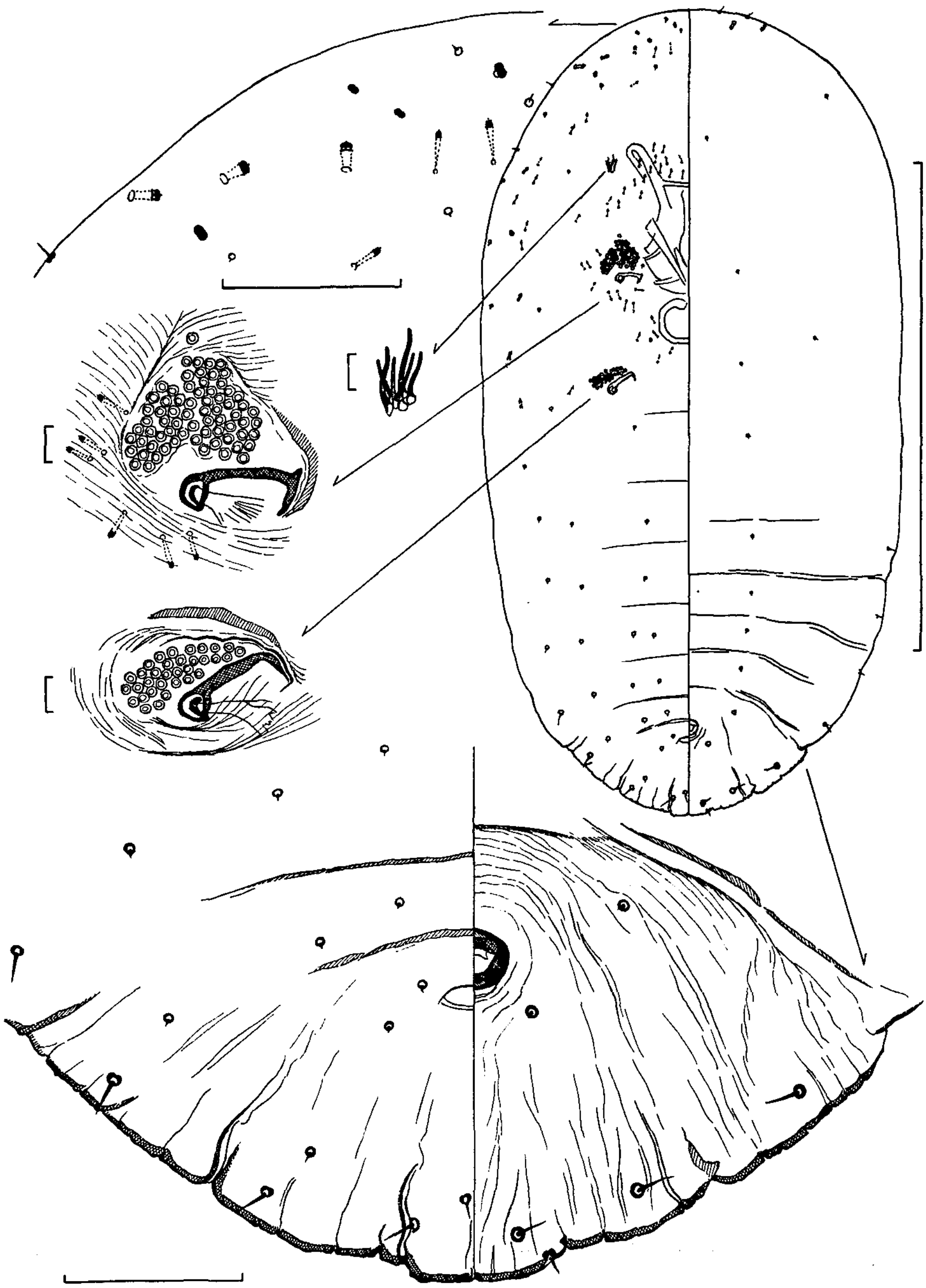

Fig. 3. *Smilacicola heimi*, 2nd instar female, oblong form. Scale for body, 0.5 mm; scales for head and pygidium, 0.05 mm; scales for antenna and spiracles, 0.01 mm.

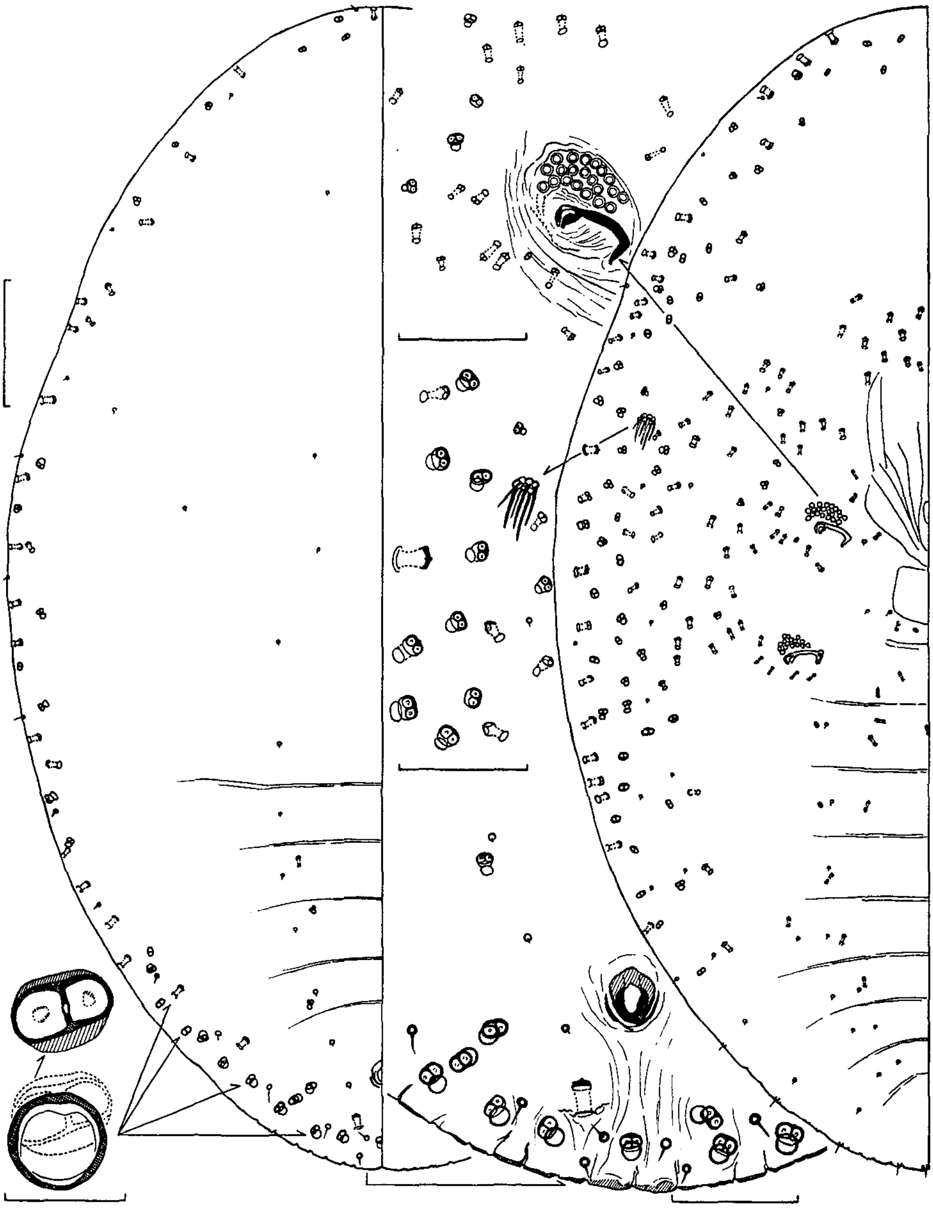

Fig. 4. *Smilacicola heimi*, 2nd instar female, circular form. Scale for body, 0.1 mm; scales for anterior spiracle, antenna, and part of pygidium, 0.05 mm; scale for enlarged duct, 0.01 mm.

Fig. 5. *Smilacicola heimi*, 2nd instar male. Scale for body, 0.1 mm; scale for pygidial margin, 0.05 mm; scales for other parts, 0.01 mm.

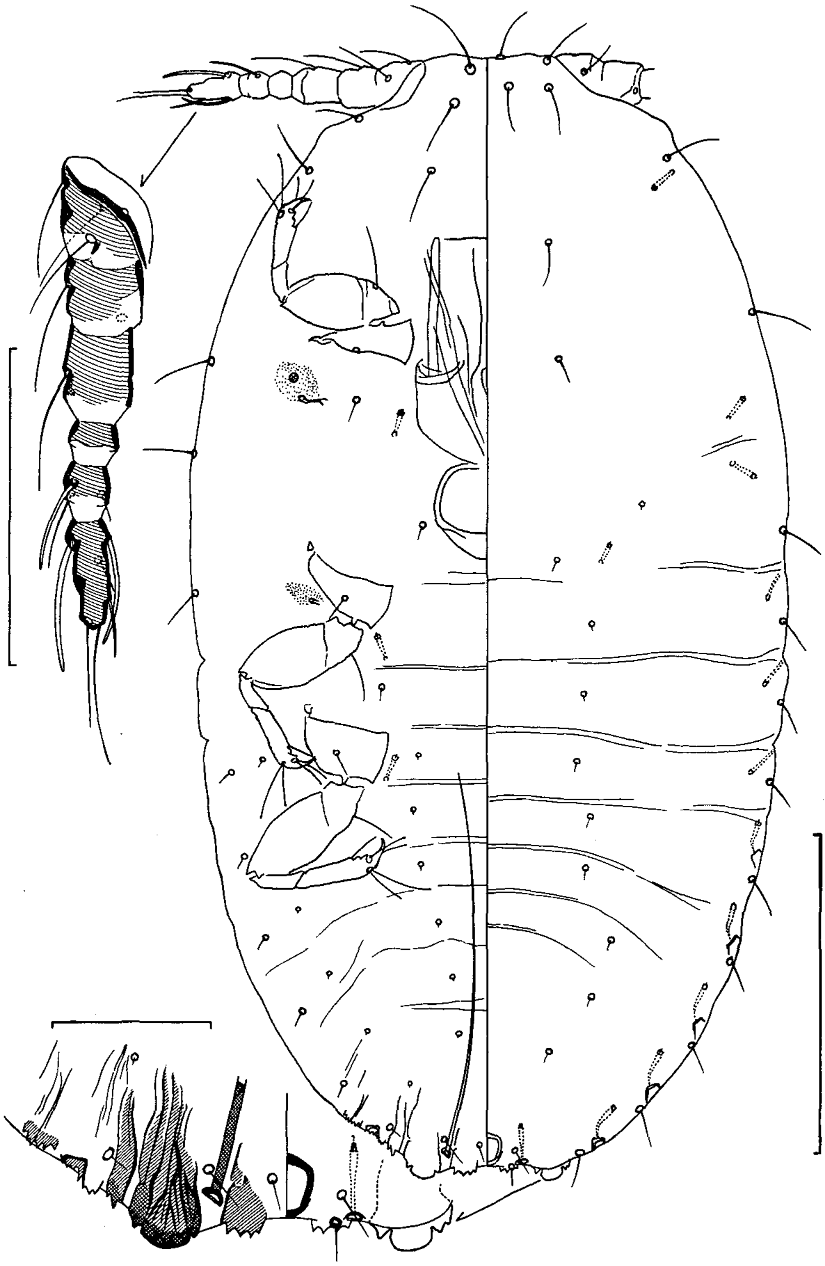

Fig. 6. *Smilacicola heimi*, 1st instar larva. Scale for body, 0.1 mm; for antenna, 0.05 mm; for part of pygidium, 0.025 mm.

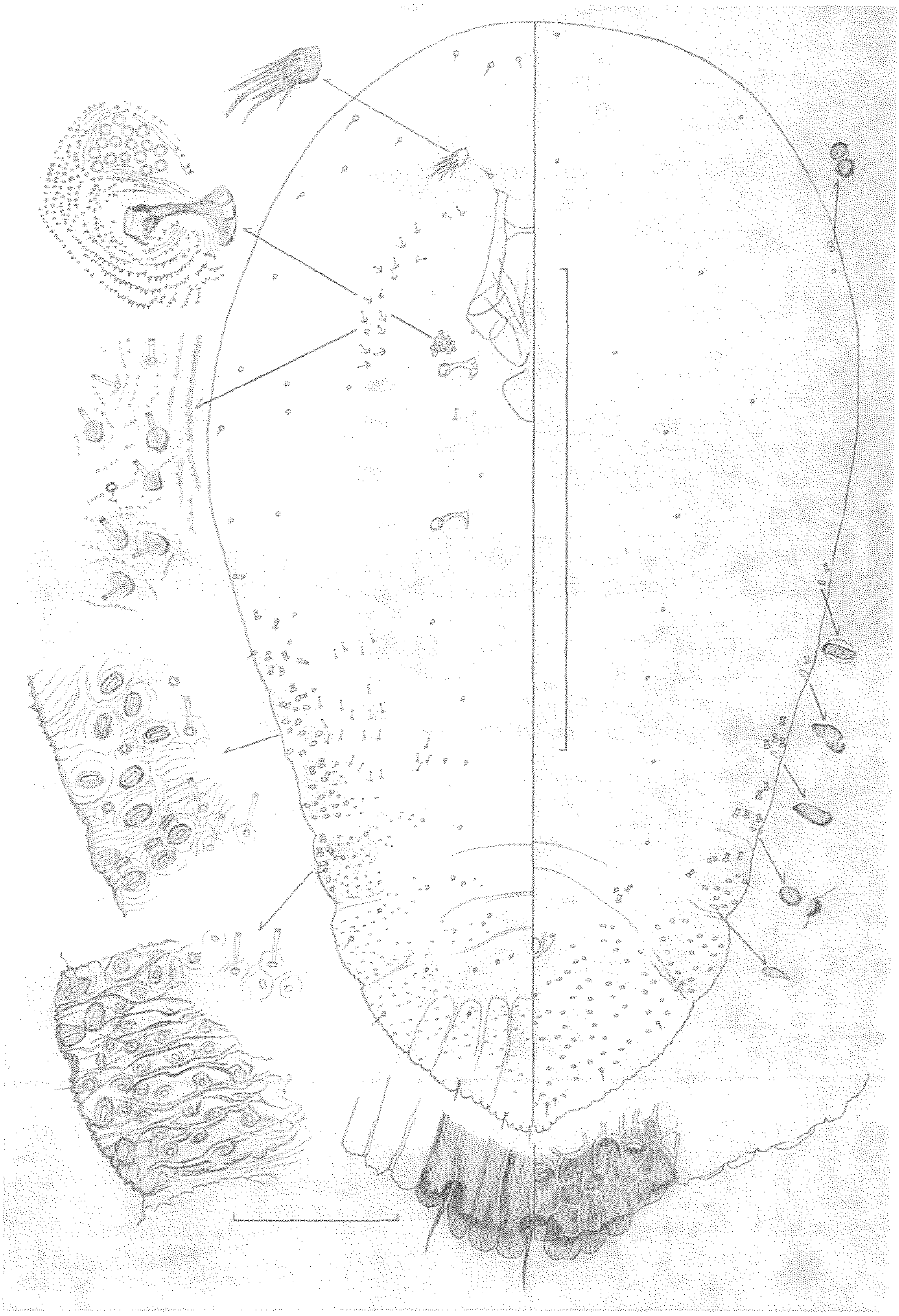

Fig. 7. *Smilacicola crenatus*, n. sp., adult female. Scale for body, 0.5 mm; for parts, 0.05 mm.

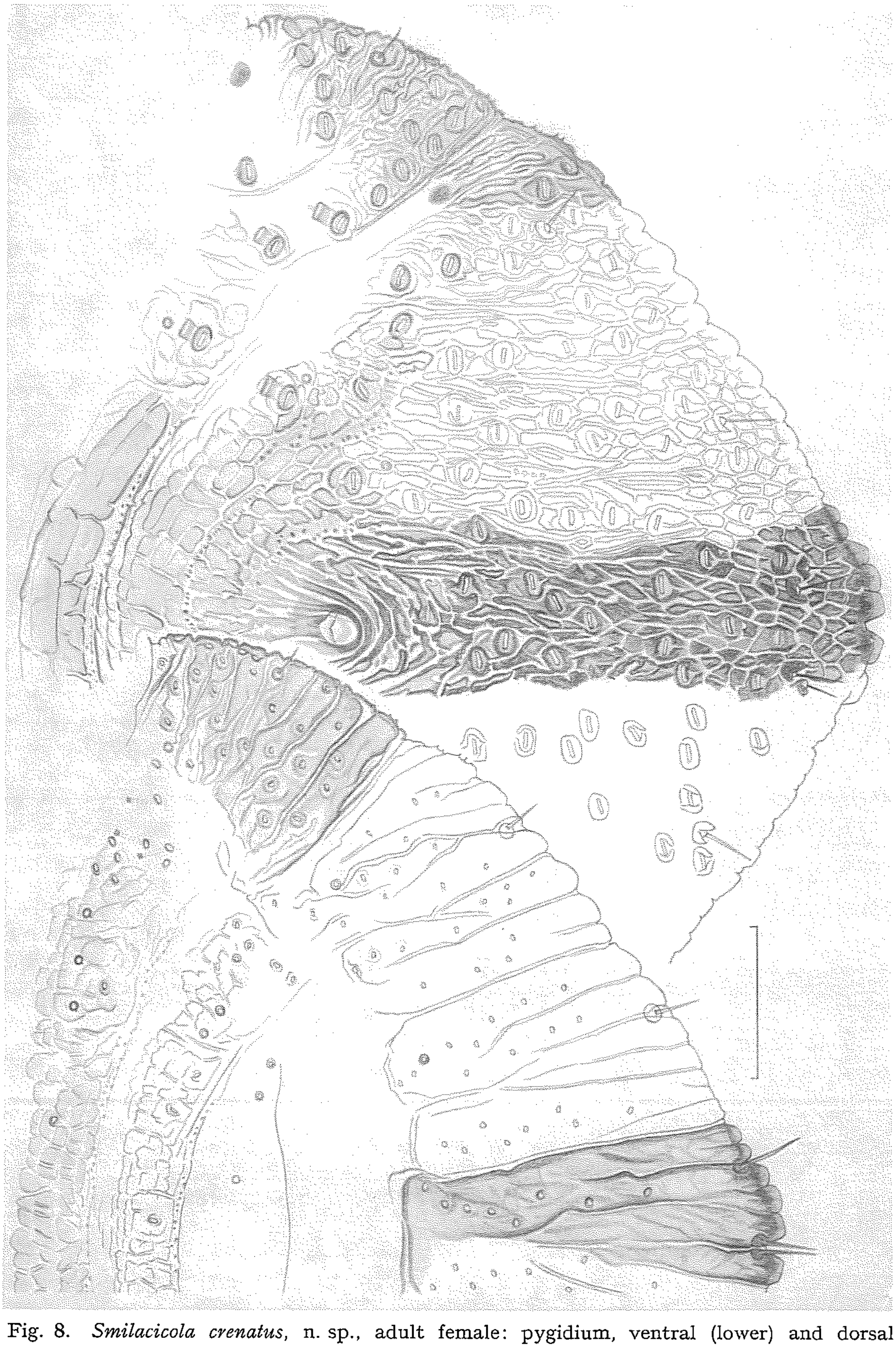

Fig. 8. *Smilacicola crenatus*, n. sp., adult female: pygidium, ventral (lower) and dorsal surface (upper). Scale, 0.05 mm.

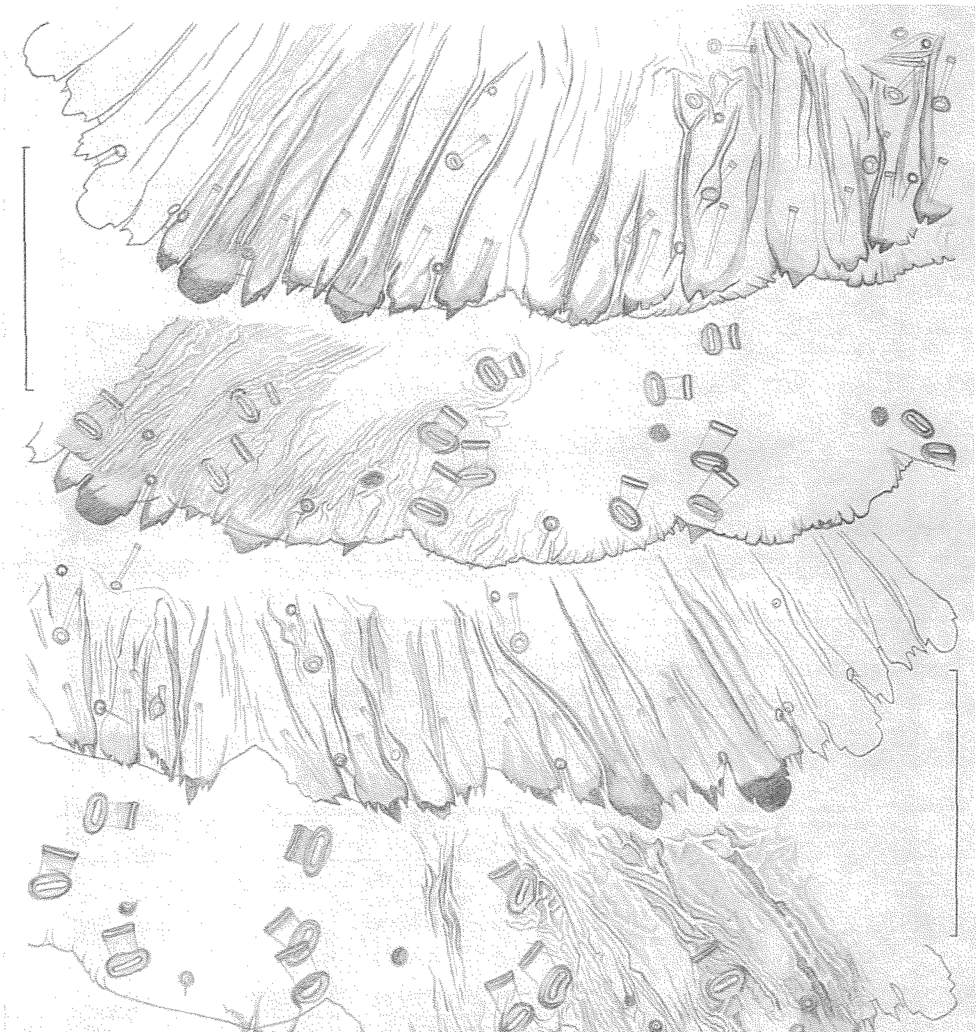

Fig. 9. *Smilacicola crenatus*, n. sp., pygidial margins of 2nd instar female (upper two: ventral and dorsal) and male (lower two: ventral and dorsal). Scales, 0.05 mm.

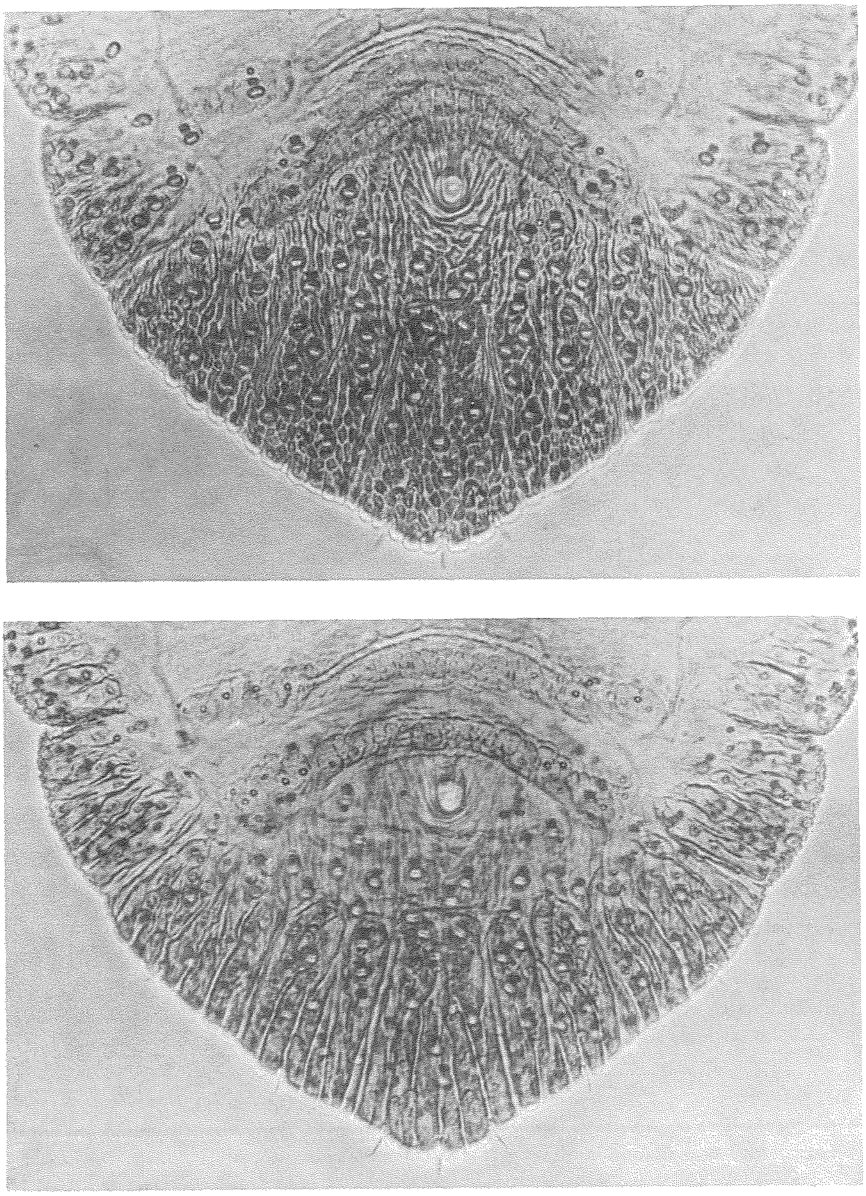

Fig. 10. *Smilacicola crenatus*, n. sp., adult female: pygidium, dorsal (upper) and ventral surface (lower).

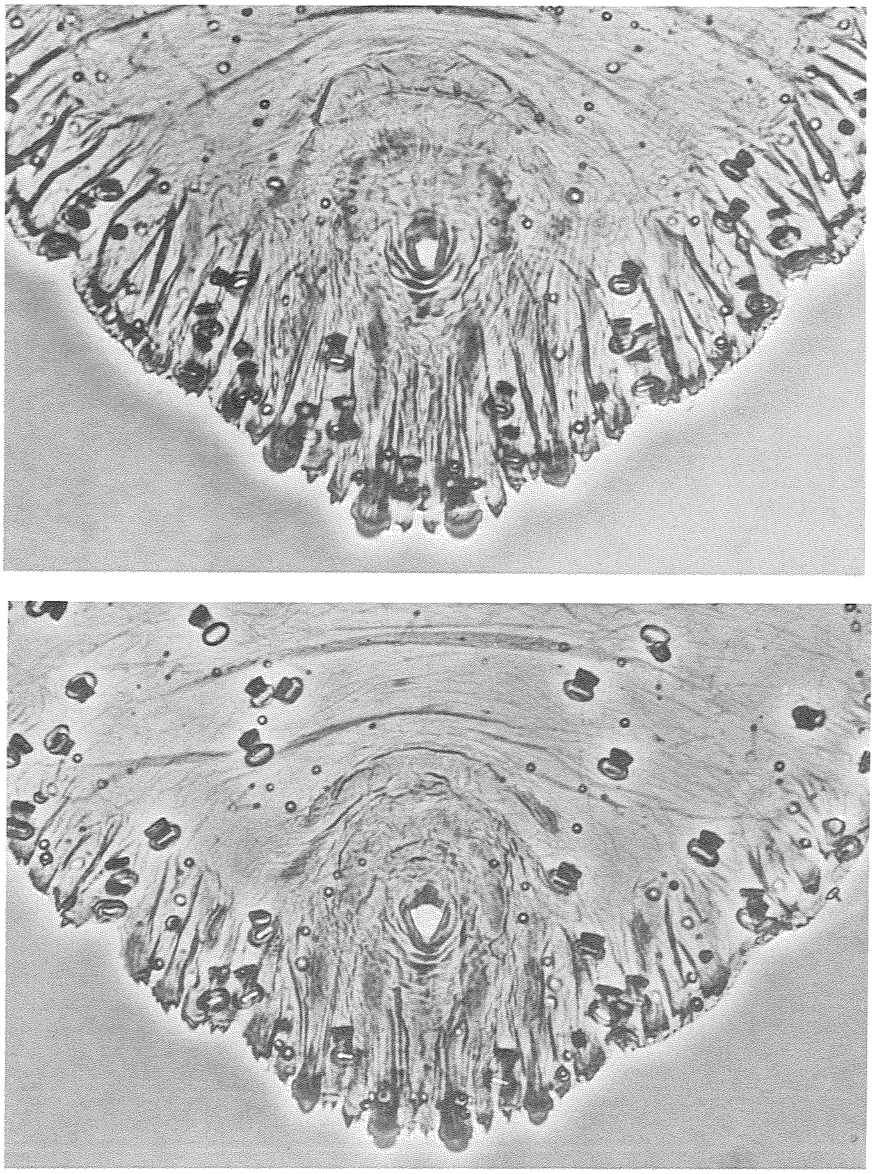

Fig. 11. *Smilacicola crenatus*, n. sp., 2nd instar female (upper) and male (lower): pygidium.

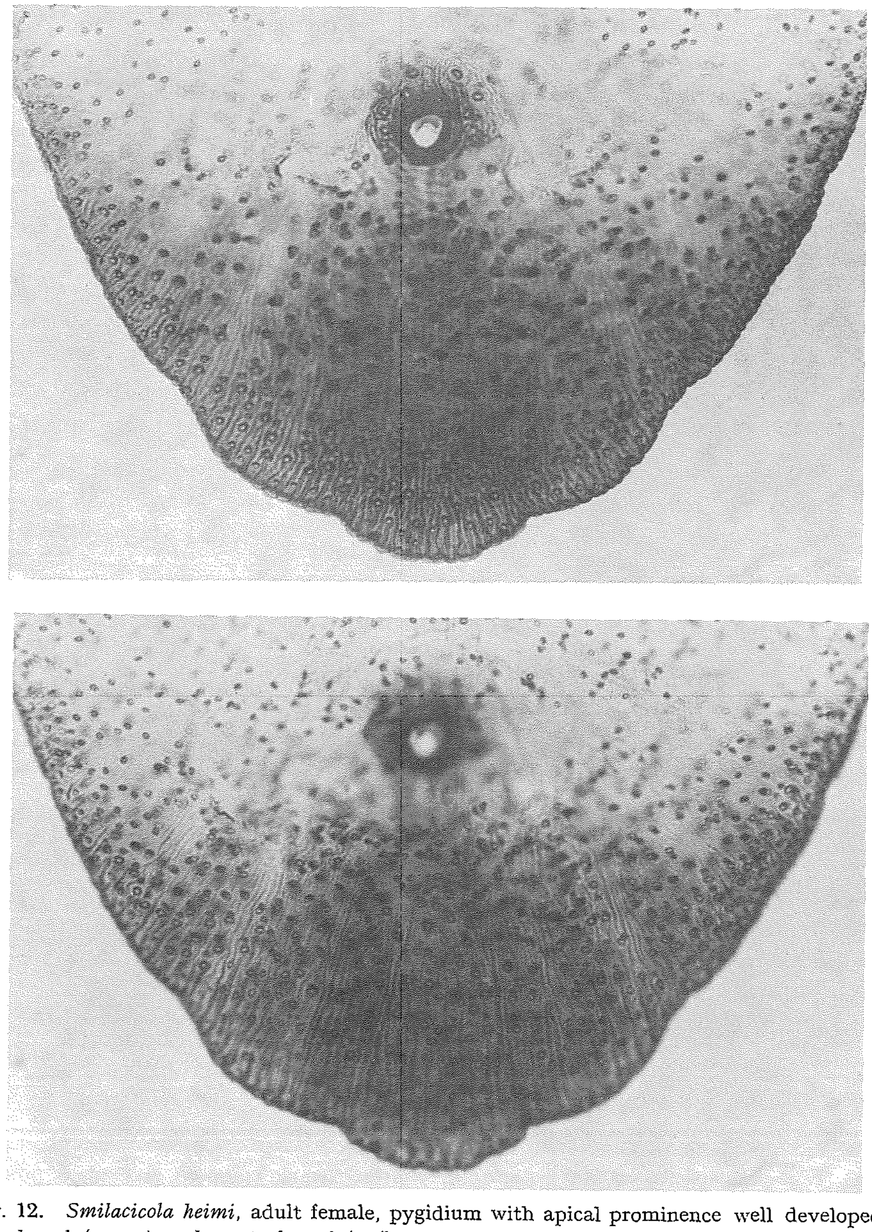

Fig. 12. *Smilacicola heimi*, adult female, pygidium with apical prominence well developed, dorsal (upper) and ventral surface (lower).

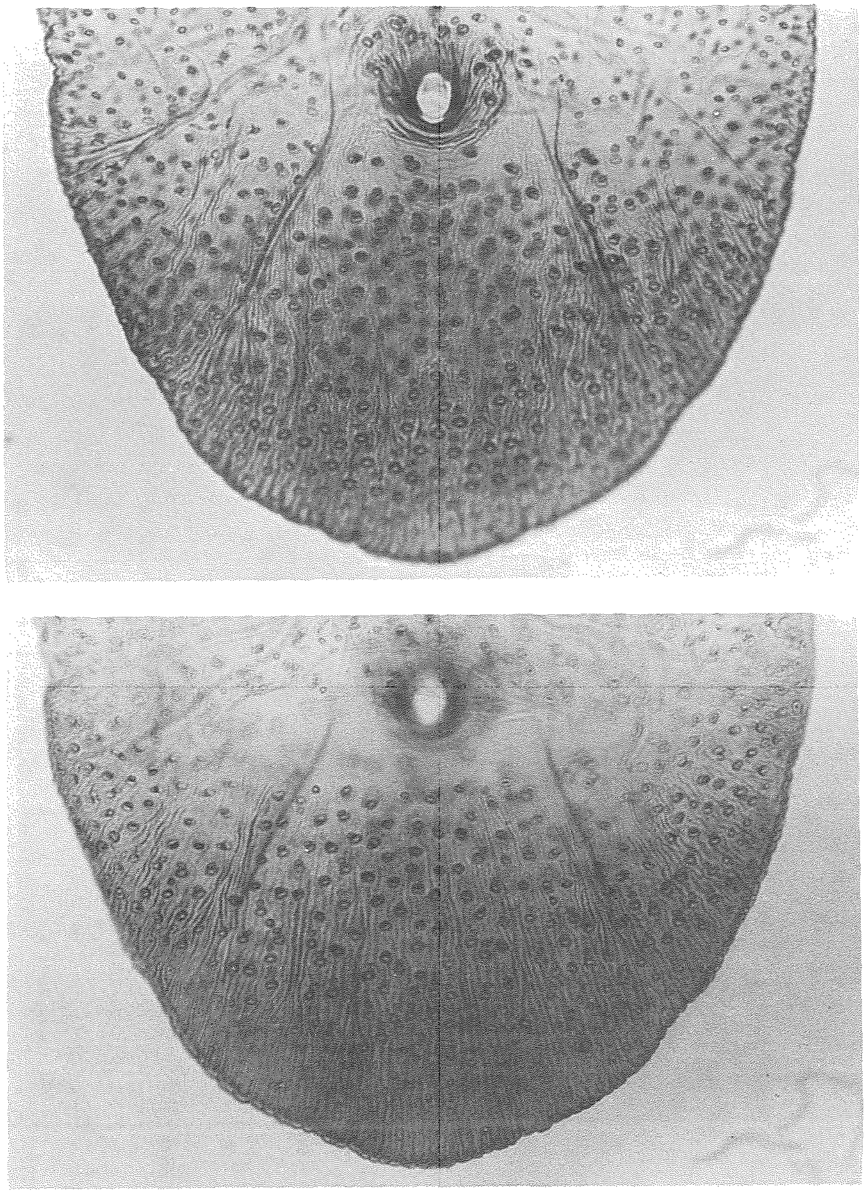

Fig. 13. *Smilacicola heimi*, adult female: pygidium with apical prominence slightly developed, dorsal (upper) and ventral surface (lower).

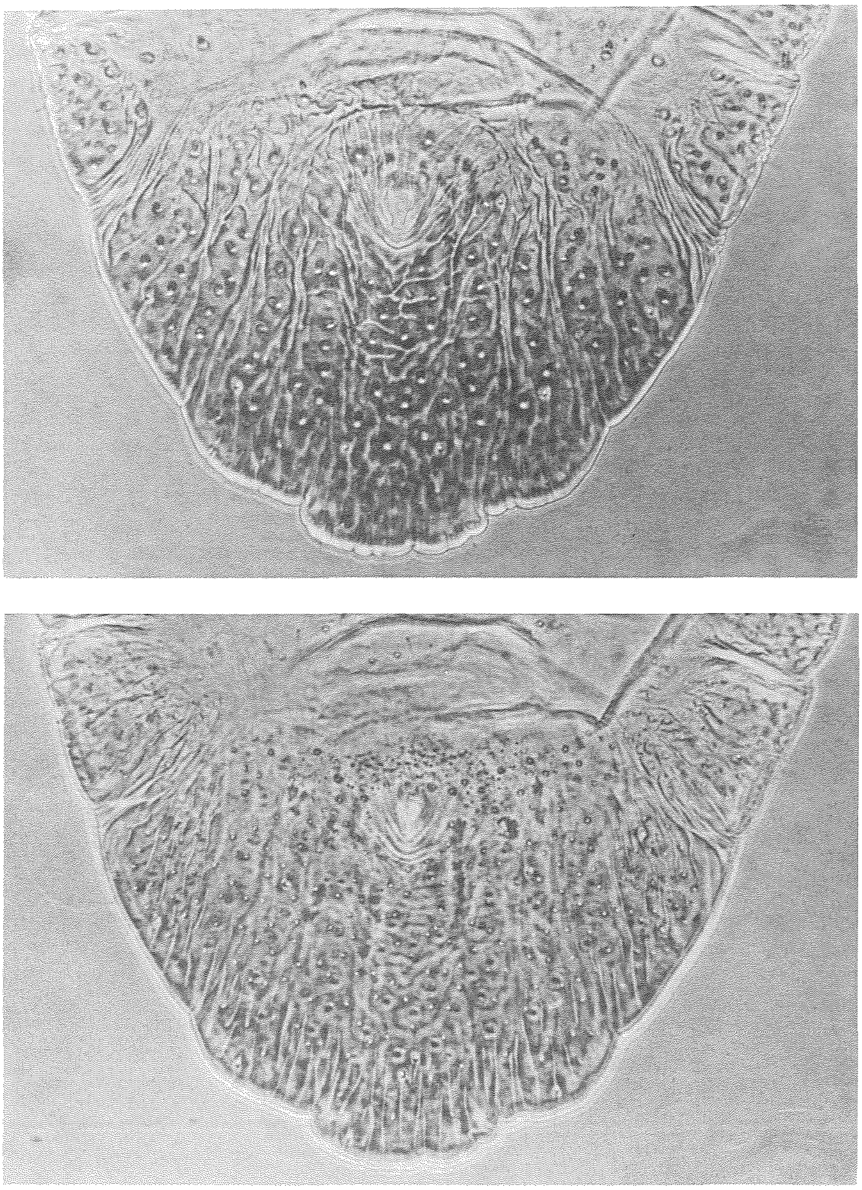

Fig. 14. *Smilacicola apicalis*, adult female: pygidium, dorsal (upper) and ventral surface (lower).